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Observations on the development of *Uncinula spiralis*.¹

B. T. GALLOWAY.

WITH PLATES XXXII AND XXXIII.

At the meeting of this Association held in Indianapolis in 1890, the writer presented a note on *Uncinula spiralis* B. & C., calling attention to a number of experiments which established the connection between the forms on *Vitis* and those on *Ampelopsis*. Since presenting the note in question some additional studies on the life history of the fungus have been made, and while these are not as complete as they might be, it is thought desirable to present the results here, especially as it is doubtful when further opportunities for work will be afforded.

The fungus in question, commonly called the grape powdery mildew, is widely distributed in this country, occurring on various species and varieties of *Vitis* and also on *Ampelopsis quinquefolia*. In California and elsewhere on the Pacific coast the fungus is especially prevalent on varieties of *Vitis vinifera*, and it also attacks these plants in the eastern United States when grown out of doors and in greenhouses. What is doubtless the same fungus occurs in Europe, where it has long been known as *Oidium Tuckeri*. The native spore form of this fungus was wanting, however, for a long time on European vines, and it is only recently that Prillieux² has noted its occurrence in France. According to Prillieux, the perithecia found in Europe do not differ materially from those occurring in this country, and so far as such evidence goes there seems no reason to doubt the statements of Viala, Scribner, and others, that the forms are identical. The present paper is concerned only with the development of the fungus in this country, the studies for the most part being made upon material from the eastern United States.

The *Uncinula* usually becomes sufficiently abundant to be easily found on cultivated varieties of grape, as well as on *Ampelopsis*, early in July. Toward the latter part of August

¹Read before section G, A. A. A. S., Springfield meeting, August, 1895.

²Sur les perithèces de l'*Uncinula spiralis* en France et l'identité de l'*Oidium* Américain et de l'*Oidium* Européen. Bull. de la Soc. Mycologique de France 9: 253. 1893.

and during the months of September and October it may be found in an active stage on leaves, fruit, tendrils, and growing shoots, covering the same with a whitish, powdery, meal-like growth, which has caused it to receive its characteristic name. The powdery appearance is due largely to the presence of the mycelium and conidia of the fungus, which develop as described below.

Mycelium.—The mycelium consists of thin-walled, nearly hyaline, sparingly septate threads, which are very variable in thickness, but average from 6 to 7μ in diameter. The threads usually run in all directions, but show a tendency to converge at certain points (fig. 1), crossing and recrossing each other until a more or less thickened mat is formed. Although the mycelium does not become noticeably abundant until July, it may be found much earlier by carefully searching vines known to be susceptible to the attacks of the fungus. It occurs on such vines soon after the leaves put out, forming more or less rounded patches, which are difficult to see without the aid of a hand lens.

Haustoria.—At numerous points on the mycelial threads, more or less lobed swellings are formed (figs. 1 and 2). These are somewhat rounded on the upper side, but next to the leaf they are flat, clinging close to the surface. These swellings are the haustoria, and from their under side fine thread-like projections grow out and into the epidermal cells of the host. Once within the cell the end of the haustorial filament swells into a bladder-like body (figs. 3 and 4), which is filled with granular matter like that in the mycelium.

Conidia.—At numerous points the mycelial filaments send up short threads, which bear the conidial spores. These are formed by successive abjunction, from three to twelve being frequently found in one chain (figs. 5 and 6). When mature the conidia are oblong (the largest diameter being 20 to 30μ and the shortest 12 to 18μ), are filled with coarse granulated matter, and frequently contain two or more large vacuoles (figs. 7 and 8), which become more sharply defined as the conidium grows older. The conidia germinate readily in moist air or water, sending out one, and sometimes several, rather thick germ tubes (figs. 9 and 10), which seldom branch unless furnished nutrient material. The production of conidia continues until late in autumn, when the growth of the fungus, as well as that of other vegetation, is checked by frosts.

Perithecia.—Perithecia, in all stages of development, may be found as early as the last of July, occurring in most cases rather evenly scattered over the parts covered by the mycelium. Owing to the close interweaving of the mycelial filaments, it is difficult to make out clearly the changes which take place in the formation of the perithecia.³ As a rule their development begins at the intersection of two or more mycelial threads. There is little regularity, however, in the matter, and nothing that could be looked upon as a sexual act. Usually short branches, with frequent septa (figs. 11 and 12) grow out from the main hyphæ. These twist around each other, forming a more or less close weft, globose in shape (figs. 13 and 14). At first the bodies are hyaline, but they soon show a brown tint and at the same time become more globular in shape. With increasing age the evidence of the short branches originating from the main hyphæ disappears, and later the walls of the peritheciæ come clearly defined (figs. 15 and 16). Soon after this there is developed from the outer walls of the perithecium eight to thirty appendages (fig. 16), which are at first hyaline and without septa, but later become brown near the base and divided by several cross walls. In the mature perithecia (figs. 17 and 18) the tips of the appendages are hooked and not unfrequently they are branched. The length of the appendages varies greatly, the form on *Vitis vinifera* from the Pacific coast (fig. 19) having especially long ones. Within the perithecia are found the ovate asci containing the spores. There are four to eight, rarely ten, asci in each perithecium, and from four to eight spores in each ascus. From studies made of imbedded material it appears that the dark-colored wall of the perithecium is composed of one or possibly two layers of somewhat thick-walled brown cells. Within this there are one or more layers of colorless cells (fig. 20a), which in the early stages at least fit close around the asci, and in some cases seem to extend into the interstices between the latter. These cells take stains in the same manner as the asci. In all the material

³After many attempts to find satisfactory material for the study of the development of the perithecia, the best results were obtained by gently boiling for half a minute small fragments of leaves containing fertile hyphæ and young perithecia in a solution of potassic hydrate. After this treatment the mycelium and young and old perithecia easily separate from the leaf and the weft of filaments may be easily floated on a slide, stained, and studied. The most satisfactory stain found was ordinary red ink diluted with 10 to 25 per cent. of its volume of water.

studied the perithecia seemed to be flattened on one side, the flattening sometimes amounting to a concavity. In such cases the asci were compressed vertically and considerably distorted. Doubtless part of the flattening was due to the shrinkage of the tissues during imbedding, but some of it was normal.

One of the principal objects of these studies was to follow the development of the fungus during the winter and to determine if possible when and how the ascospores germinated and the manner in which the host was infected in spring. It was deemed especially desirable to germinate the ascospores, as the evidence as to how this takes place in the *Erysipheæ* is comparatively meager. Leaves of both ampelopsis and vitis containing the perithecia of the uncinula were collected in the autumn and stored in several ways. Some were placed on the ground and covered with stones and boards, while others were tied up in cheese cloth sacks and the sacks were then thrown on the ground out of doors and tied to stakes in order to prevent them from blowing away. This last method was found to be most satisfactory, as when the leaves were covered with boards they rotted so badly that most of the perithecia were lost. Frequent examinations were made of debris under vines which had been attacked by the uncinula the previous summer. No material of value, however, was obtained in this way, all traces of perithecia disappearing early in December.

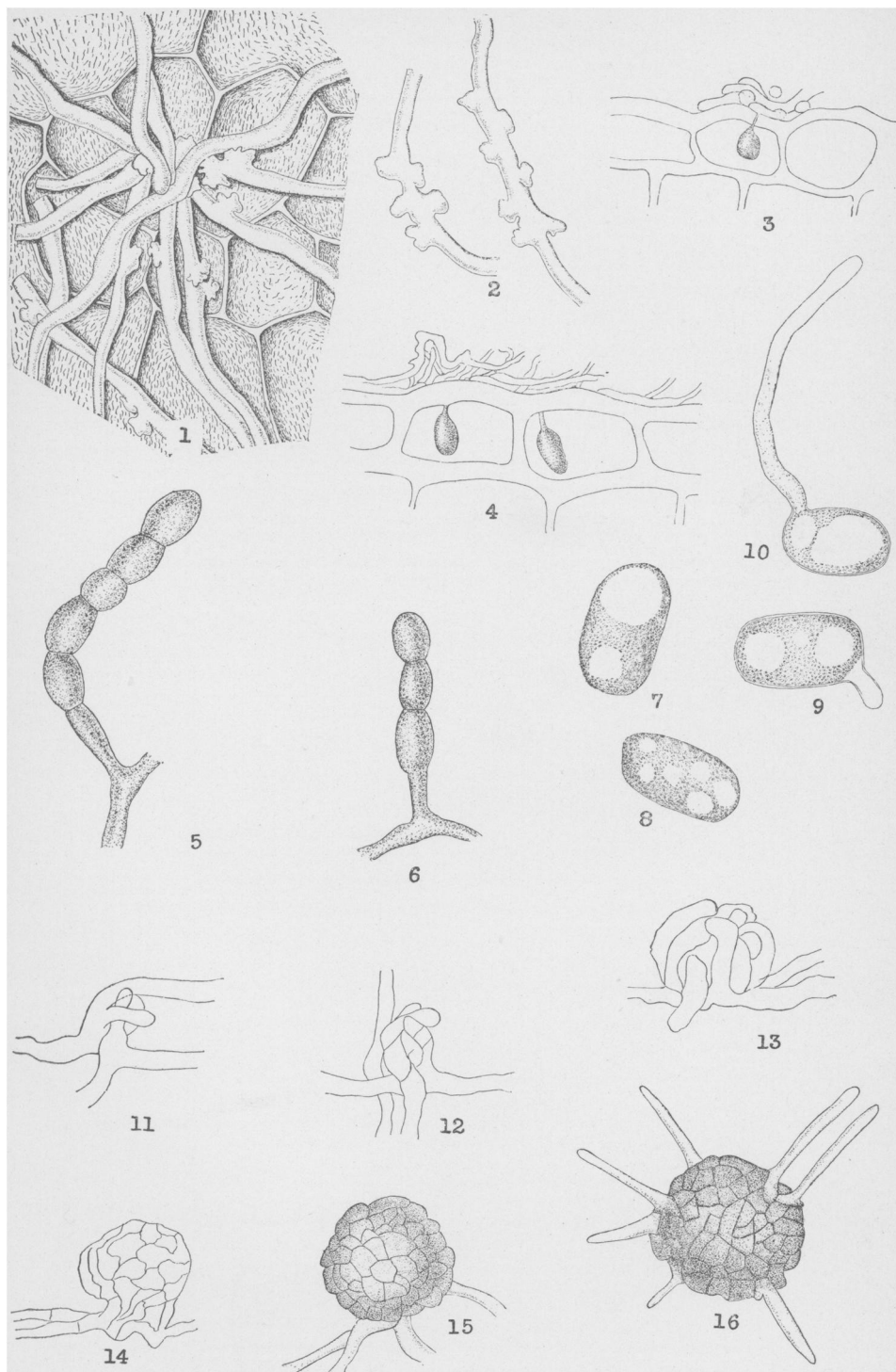
The first change of importance in the perithecia was the disappearance of the appendages. After December 1st it was rare to find a perithecium with all of its appendages intact. The hooked ends are usually the first to break off and soon the entire appendage disappears. The asci and spores undergo little change until the last of December, when many of them are found dead or more or less collapsed. All attempts to germinate the ascospores before January failed, and it was only after repeated trials through the months of February and March that success was attained.

The perithecia were from time to time removed from the leaves which had been exposed to the weather and placed in Van Tieghem cells, in the bottom of which was a drop of sterile water. Under these conditions the perithecia were kept properly moistened and could be examined with the microscope at any time. Perithecia collected after January 1st

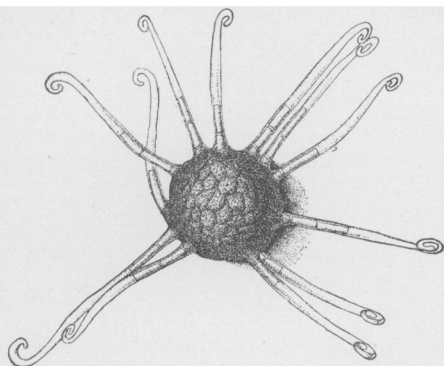
and kept in Van Tieghem cells, as described, showed little or no change if allowed to remain perfectly quiet.⁴

After standing from a few days to a week or more, however, a slight jar was often sufficient to cause the perithecia to rupture and the asci and ascospores to escape. When this took place probably 8 per cent. of the ascospores collapsed, while the remainder either made no change or in the course of three or four hours began to send out germ tubes. The following case, which differs but little from others observed, illustrates the matter under consideration. Perithecia from the open ground were placed in Van Tieghem cells on January 7th. Twenty days later no change had taken place, the cell having been kept free from jars and other disturbances. The cell was then placed under the microscope and gently jarred with a needle, whereupon one of the perithecia suddenly burst and the asci began to escape into the drop of water surrounding the mass. The first ascus was violently ejected from the perithecium to a distance equal to about twice the length of the former. This was immediately followed by a second and a third ejected in the same way (fig. 21). The ruptured wall of the perithecium then closed and no more asci escaped. In coming through the ruptured walls of the perithecium the asci were more or less constricted, but they immediately assumed their normal shape as soon as they were entirely free. No sooner were the asci free than their spores began to escape or else to break up within the ascus. In the former case they escaped from the top, side, or bottom in much the same way as did the asci, but with less force. A large part of the spores burst as soon as they were free from the asci. In bursting the spores literally flew to pieces, the walls and contents being scattered in all directions. Nearly all the spores that failed to burst began to send out germ tubes in four or five hours, and at the end of twelve hours the tubes (fig. 22) had reached a length twice that of the spore or more. From a number of observations it appears that the sudden ejection of the asci is largely due to the abrupt contraction of the walls

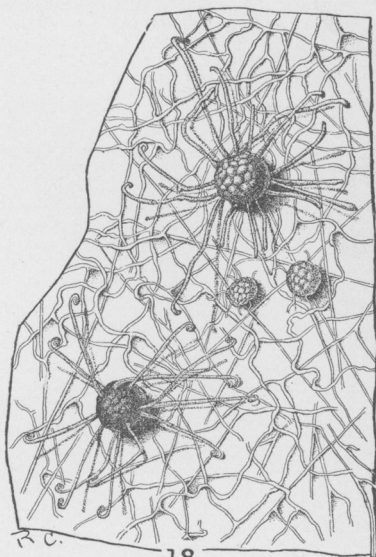
⁴It was not uncommon to find perithecia which had been kept in water sending out long, hyaline filaments from the outer walls. At first it was believed that the spores within the asci had germinated and pushed their germ tubes through the perithecial walls. That this was not the case, however, was shown by the fact that when ruptured the asci and spores within were found in a normal condition. From the evidence at hand it seems more than likely that the mycelial filaments were direct outgrowths from the stroma-like wall of the perithecium. This matter, however, requires further study.



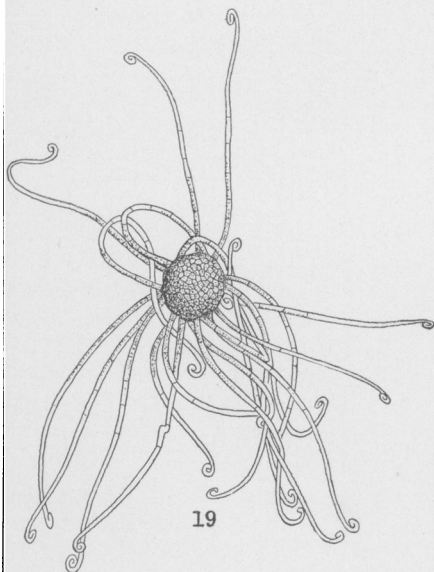
GALLOWAY on UNCINULA.



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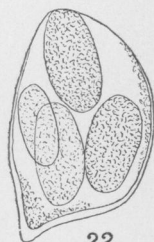
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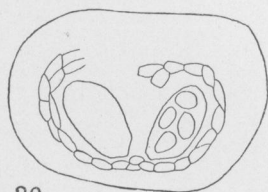
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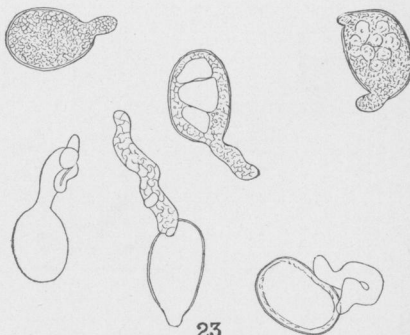
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23

of the perithecium after being ruptured. The perithecium is doubtless filled to the point of bursting, pressure being greatest just over the apices of the asci. The least disturbance at this stage will cause a rupture at the point above noted and immediately the asci begin to go in the direction of the least resistance. During the passage of the thickest part of the ascus (*i. e.* the top), it moves quite slowly, and at this time the ruptured edges of the perithecium are pushed a little further apart. As soon, however, as the tapering portion of the ascus is reached there is a sudden contraction of the more or less elastic perithecial walls and in consequence the ascus is ejected with considerable force. After April 1st it was difficult to find perithecia containing spores and before the end of the month they had entirely disappeared. A number of attempts were made to infect grape and *Ampelopsis* leaves with ascospores, but the results of this work were in every case negative.

In conclusion I wish to express my thanks to Mr. D. G. Fairchild, my former assistant, who made a number of the sketches upon which the finished drawings accompanying this paper are based, and who also aided me in other ways.

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EXPLANATION OF PLATES XXXII AND XXXIII.

Fig. 1. Portion of upper surface of *Ampelopsis* leaf showing mycelium and haustoria.—Fig. 2. Isolated pieces of mycelium showing upper surface of haustoria.—Figs. 3 and 4. Haustoria within the epidermal cells of *Ampelopsis quinquefolia*.—Figs. 5 and 6. Chains of conidia.—Figs. 7 and 8. Isolated conidia.—Figs. 9 and 10. Germinating conidia.—Figs. 11–17. Development of perithecia on *Ampelopsis*.—Fig. 18. Portion of *Ampelopsis* leaf showing perithecia in different stages of growth.—Fig. 19. Perithecium from leaves of *Vitis*.—Fig. 20. Section of mature perithecium showing asci and colorless cells surrounding them.—Fig. 21. Perithecium which has just burst, showing relative position of ejected asci.—Fig. 22. Ascus containing four spores, drawn just before the escape of the latter.—Fig. 23. Germinating ascospores.